

Networking nutrients: how nutrition determines the structure of ecological networks

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Abstract

Nutrients are a critical driver of ecological interactions (e.g., plant-herbivore, predator-prey and host-parasite) but are not yet integrated into ecological networks. Ecological concepts like nutrient-specific foraging and nutrient-dependent functional responses provide invaluable mechanistic context to complex ecological interactions. These concepts in turn offer an opportunity to predict dynamic network processes such as interaction rewiring and cascading extinction events. Here, we propose the concept of nutritional networks. By integrating nutritional data into ecological networks, we envisage significant advances to our understanding of ecological dynamics at every scale from individuals to ecosystems. We summarise the potential influence of nutrients on the structure and complexity of ecological networks, with specific reference to niche partitioning, predator-prey dynamics, spatiotemporal patterns and robustness. Using an empirical example of an inter-specific trophic network, we show that networks can be constructed with nutritional data to disentangle the drivers of ecological interactions in natural systems. Throughout, we identify fundamental ecological hypotheses that can be explored in a nutritional network context, and highlight methodological frameworks to facilitate their operationalisation.

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Abstract

Nutrients are a critical driver of species interactions (e.g., plant-herbivore, predator-prey and host-parasite) but are not yet integrated into network ecology analyses. Ecological concepts like nutrient-specific foraging and nutrient-dependent functional responses could provide a mechanistic context for complex ecological interactions. These concepts in turn offer an opportunity to predict dynamic network processes such as interaction rewiring and extinction cascades. Here, we propose the concept of nutritional networks. By integrating nutritional data into ecological networks, we envisage significant advances to our understanding of ecological dynamics from individuals to ecosystem scales. We summarise the potential influence of nutrients on the structure and complexity of ecological networks, with specific reference to niche partitioning, predator-prey dynamics, spatiotemporal patterns and robustness. Using an empirical example of an inter-specific trophic network, we show that networks can be constructed with nutritional data to illuminate how nutrients may drive ecological interactions in natural systems. Throughout, we identify fundamental ecological hypotheses that can be explored in a nutritional network context and highlight methodological frameworks to facilitate their operationalisation.

Keywords: food webs, network ecology, macronutrients, multilayer networks, nutritional networks, trophic interactions.

Introduction

The nutrient content of animals, measured through elements or macronutrients, underpins many biological processes, and each nutrient performs a distinct set of roles, from energy provision to cell signalling (Elser

& Sterner, 2002; Roeder & Behmer, 2014; Simpson & Raubenheimer, 2012). Nutrition has long been associated with ecology and integrated into studies of ecological interactions (Lihoreau et al., 2015; Simpson, Raubenheimer, Charleston, & Clissold, 2010) from dietary choice by individual foragers to flows of elements through entire ecosystems (Elser & Sterner, 2002; Raubenheimer et al., 2009; Simpson & Raubenheimer, 2012). These studies have often focused on specific taxa or contexts, such as nutrient-based prey choice in spiders (Rendon *et al.* 2019), balancing of macronutrient intake by mink (Mayntz *et al.* 2009), compensatory feeding in beetles following diapause (Raubenheimer, Mayntz, Simpson, & Toft, 2007), nutrient recycling by zooplankton and fish (Elser & Urabe, 1999) or trophic cascades in lakes (Elser, Chrzanowski, Sterner, & Mills, 1998). Despite the wealth of research concerning the impact of nutrients on individual species interactions, nutrition has been integrated far less across some subfields (Pyke, Pulliam, & Charnov, 1977; Raubenheimer et al., 2009); in particular, relatively little is known about how nutrition influences the dynamics of entire communities of interacting species within ecological networks.

Nutrients have the potential to influence communities and ecosystems by influencing the processes underpinning ecological interactions, such as foraging behaviour and physiology (Elser et al., 1998; Machovsky-Capuska, Coogan, Simpson, & Raubenheimer, 2016; Machovsky-Capuska et al., 2018; Potter, Stannard, Greenville, & Dickman, 2018). Certainly, the importance of nutrients for interactions has been demonstrated at various scales of organisation; for example, from the interactions between individual social insects up to the collective behaviour of superorganisms (Lihoreau et al., 2015, 2014, 2017). Despite the elementary nature of nutrients for trophic interactions, most food-web studies focus on energy transfer and few studies have quantified nutrients in the context of interspecific interaction networks, the examples largely restricted to social networks (Senior *et al.* 2016). Whilst nodes within networks have traditionally comprised taxonomic units, the increasingly common integration of other ecological information to rationalise interactions, i.e., trait data (Woodward *et al.* 2005; Junker *et al.* 2012; Eklöf *et al.* 2013), presents a timely opportunity for the incorporation of nutritional context into ecological networks.

Here, we describe: (i) the mechanisms underpinning the effects of nutrients on ecological networks, (ii) how these potentially manifest in network structures and functions, and (iii) the ecological context that can be gained from the inclusion of nutrients in network analyses. We first examine how nutrients are likely to affect the structure and function of ecological networks, from individual foraging to landscape-scale effects, and the concepts underpinning nutrient data in a network context. We focus on macronutrients (i.e., proteins, lipids and carbohydrates) in trophic interactions and food webs given the greater body of work underpinning nutrients in this context; however, the concepts and ideas presented here apply more widely to other ecological interactions, such as pollination, seed-dispersal and parasitism, which are also motivated by nutrients (Zuzarte-Luís & Mota 2018; Ruedenauer *et al.* 2019; Lei *et al.* 2021). Throughout, we argue that integrating nutrients into networks represents a critical frontier for ecology, facilitating a mechanistic exploration of complex ecological systems through a new lens which may in turn resolve unexplained drivers of ecological interactions. We outline several means for implementing and representing nutrient data in networks to guide others in constructing ecological networks with greater explanatory and predictive power in natural systems.

How nutrients influence ecological interactions

Networks form at all levels of biological organisation (Guimarães 2020) and nutrients impact those networks through different mechanisms at each scale. Throughout, we highlight the nutritional mechanisms driving different network properties (Table 1). This range of potential mechanisms linking nutrients to ecological networks are often evidenced by existing literature but others are yet to be substantially supported by empirical data despite the logic underlying these hypotheses. Individuals and populations provide an intuitive scale at which to understand the mechanistic role of nutrients in ecological systems. Thus, in this section, we review how different processes (e.g., nutrient-specific foraging, functional responses, behaviours and adaptations) influence trophic interactions and the subsequent individual and population level effects, with the aim of providing a mechanistic basis for the subsequent discussion on how nutrients structure inter-specific

ecological interaction networks.

Table 1: Examples of nutrient-mediated ecological processes and their effects on the structure of ecological networks. We provide a mechanistic explanation for the effects that nutrients may have upon node degree (the number of nodes with which a given node interacts), generality (the number of resources a consumer interacts with), vulnerability (the number of consumers a resource interacts with), nestedness (the extent to which a consumer’s interactions form a subset of those of other consumers), modularity (the extent to which a network is divided by distinct modules of interactions), link density (the number of unique interactions in the network), interaction evenness (how evenly spread interactions are across nodes) and robustness (how many secondary extinctions are likely per primary extinction).

Scale	Network properties	Ecological driver(s)	Nutritional mechanism
Node	Degree	Nutrient-specific foraging	The greater the proportion of nutritional generalists (ge
	Generality	Nutrient-specific foraging Nutritional naivety	At least for generalist foragers, nutrient-specific foraging Nutritionally naïve foragers, such as recent migrants, ma
Network	Centrality	Nutrient limitation	Taxa rich in nutrients limited in the environment will be
	Nestedness	Generalism versus specialism	Nutritional specialists interact with a subset of the resou
	Modularity	Nutrient-specific foraging	Animals will exploit a subset of resources to obtain opti
		Specialism	If specialists interact with unique subsets of the resourc
	Link density	Nutrient-specific foraging	Generalists will redress nutritional imbalances through r
	Interaction evenness	Nutrient limitation	In environments with limited availability of one of more
Nutrient-specific foraging		Generalists will redress nutritional imbalances by feedin	
Robustness	Nutrient limitation	Systems with limited provision of one or more nutrients	

Nutrient-specific foraging determines the identity of interactions

At the individual level, foragers may alter their behaviours and interactions with other organisms to redress nutritional deficiencies through nutrient-specific foraging (Table 1), first demonstrated in invertebrate predators including carabid beetles and spiders by Mayntz, Raubenheimer, Salomon, Toft, & Simpson (2005). Whilst individual foragers are thought to optimise their nutrient intake and thus select resources that satisfy their nutritional needs (Mayntz *et al.* 2005; Jensen *et al.* 2012; Cuff *et al.* 2022c), many factors determine the diversity of resources that a consumer interacts with in an environment.

Trophic generalism or specialism (i.e., dietary niche breadth and the balance of different resources used by an organism) is elementary in a nutritional context, since consumers are physiologically, metabolically and behaviourally adapted to acquire nutrition either from a relatively narrow taxonomic niche or from a broad range of taxa (Despland & Noseworthy, 2006; Lee, Simpson, & Raubenheimer, 2005; Raubenheimer & Simpson, 2003; Simpson, Raubenheimer, Behmer, Whitworth, & Wright, 2002). Despland & Noseworthy, (2006), for example, demonstrated that forest tent caterpillars, *Malacosoma disstria*, which are usually restricted to a single host plant and thus experience minimal nutritional variation, do not exhibit compensatory feeding (i.e., feeding on an alternative food source) when deficient in a particular nutrient. Specialists forage for their specific resources more efficiently (i.e., in a focused and behaviourally optimised manner), facilitating consumption of resources less accessible to generalists, to continually maintain a nutritional optimum. Garcia *et al.*, (2018), for example, showed that the specialist spider *Nops cf. variabilis* immobilised prey faster, overcame larger prey and gained more proportional mass than the generalist spider *Harpactea rubicunda*. Generalists are thought to consume a greater quantity and range of resources since these resources may not always be nutritionally optimal (Pompozzi *et al.* 2019; Rendon *et al.* 2019; Cuff *et al.* 2022c).

Assuming that nutrition is an important driver of trophic interactions, these patterns effectively predicate that specialists will feed on nutritionally similar resources from which they are physiologically adapted to extract their nutritional requirements. Generalists, however, will reactively forage for different resources to redress imbalances in nutrient assimilation, or will at least consume a diverse range of resources and

stochastically balance nutrient intake. As a consequence, specialists and generalists respond to dietary imbalances differently, with generalists more likely to overconsume imbalanced resources as they have a higher chance of encountering complementary imbalanced resources in the future, relative to specialists whose diet is less variable (Raubenheimer & Simpson, 2003; Simpson & Raubenheimer, 2012). Nutrient availability and resource use at an individual level is likely to generate the patterns of generalists and specialists within interaction networks, potentially resulting in modular networks between specialists and nestedness of specialist interactions within those of generalists. Furthermore, the level of nutritional specialisation will have impacts on an organism’s ability to adapt within an ecological network following a loss of resources. Generalists are more likely to flexibly respond to a loss of resource than a specialist, for example (Table 1).

Interaction strengths are a product of functional responses

The behavioural responses of individual consumers are likely to manifest at the population level in the form of functional responses to different resources (Holling 1966). Functional responses, which are effectively how a consumer’s interaction with a resource responds to changes in its abundance, have been linked to nutrients before; specifically, a ‘type IV’ dome-shaped relationship and nutritional saturation (Bressendorf & Toft 2011). Functional responses have also been shown to be affected by the nutritional content of prey and the prior diet history of predators (Schmidt *et al.* 2012). It is, however, likely that nutritional dependence of functional responses extends to other functional response types, and thus form the mechanistic basis of nutrient-specific foraging (Figure 1).

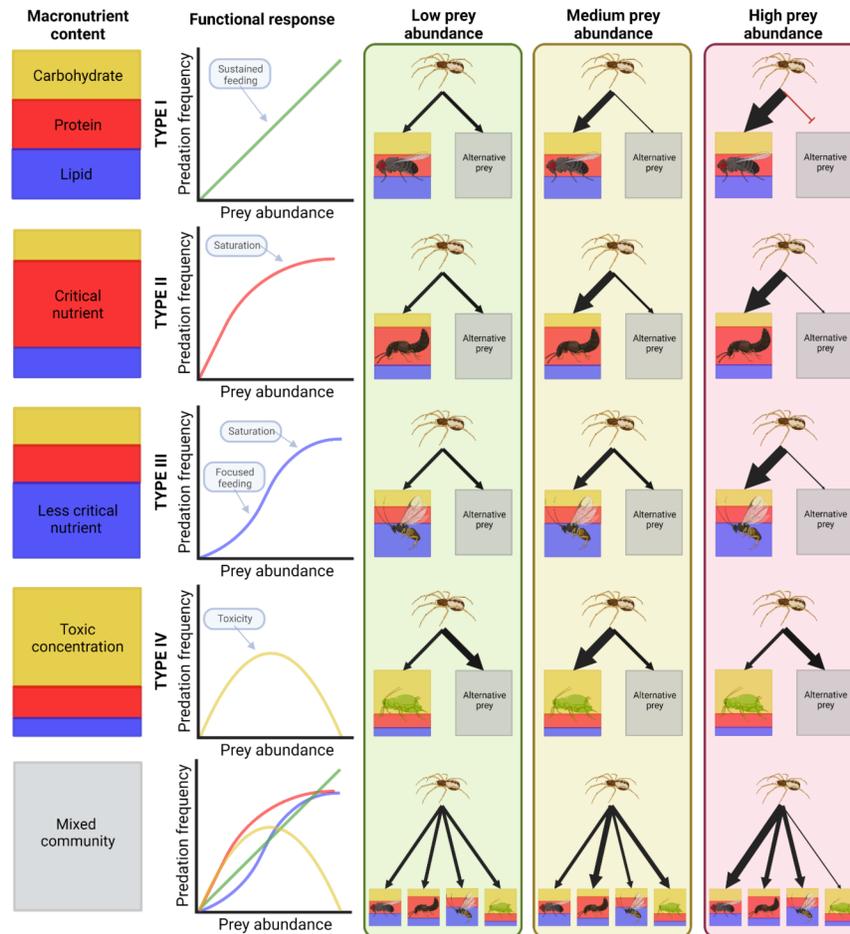


Figure 1: How functional responses might reflect different nutrient contents and how this may manifest in network topologies. Example networks are given in which spiders are predating nutritionally dissimilar prey. Nutritionally balanced resources may be linearly exploited by predators since they provide all of the nutrients required by the consumer. If a resource contains more of a particular nutrient that might be especially critical to the development or survival of the consumer, it may be disproportionately consumed until the consumer is saturated with that nutrient. If a nutrient is less critical but still important for survival, this may similarly experience focused exploitation and saturation, but only once resource density reaches a point at which adjusted foraging becomes a valid investment. If a resource is rich in toxins or contains a concentration of a nutrient that may become toxic with focused feeding (e.g., carbohydrate in sap-feeding insects), exploitation may increase until experience of the toxicity or saturation with that nutrient allows the consumer to seek alternative sources. Figure created in Biorender.com.

A ‘type I’ response may suggest a balanced resource nutritional profile that matches the requirements of the consumer. A ‘type II’ functional response may be indicative of a high concentration of a nutrient critical for survival or development. A ‘type III’ functional response may be indicative of a resource rich in a secondarily important nutrient that can be obtained passively from other resources for which focused feeding is only lucrative at higher abundances. A ‘type IV’ response is indicative of a nutrient that is possibly toxic at higher concentrations or co-occurs with a toxin, and has been demonstrated in wild populations of animals in this context (Bressendorf & Toft 2011; Cuff *et al.* 2022b). All of these responses will, however, be modulated by a multitude of other factors such as defences, toxins and ease-of-capture, discussed in more detail below.

By extending this understanding of functional responses to a nutritional context, it may be possible to predict how foragers react to dynamic species assemblages and how nutrients may factor into investigations of foraging ecology. From a network perspective, the weightings of particular links may change depending on this nutritional context, particularly when considered alongside resource abundance, wider trait data and, ideally, analysis of density-dependence of resource choice (Vaughan *et al.* 2018). Furthermore, these responses may explain temporal variation in interaction strengths, depending on the population dynamics of the interacting species. It might be possible to refine predictions of interaction frequencies based on these data and concepts, to the benefit of theoretical network construction and rationalisation of network structures in empirical networks.

How nutrients influence the structure of ecological networks

Nutrient-driven processes at individual or population levels will ultimately influence ecological interactions across multiple trophic levels, forming a cascade of nutrients from basal resources to apex predators (Elser *et al.*, 1998; Raubenheimer *et al.*, 2009; Wilder, Norris, Lee, Raubenheimer, & Simpson, 2013). The patterns observed between individual pairs of interacting species will upscale to form a wider network influenced by nutrient-driven identity and strength of the underlying interactions. It is important to identify if the larger-scale consequences of these interactions arise due to emergent effects produced as a result of nutritional interactions. Across ecosystems, nutritional changes can generate bottom-up effects on community structure and top-down effects via modulated predator abundance and fitness (Fountain *et al.* 2008, 2009). By understanding the mechanisms by which nutrients affect network structure at different scales, we can assess and predict how networks may respond to dynamic nutritional processes.

Ecological network structure may reflect nutrient availability and demand

Varying nutrient requirements between taxa drives their exploitation of different resources and occupation of different trophic and nutritional niches (Behmer & Joern, 2008), in turn facilitating the formation of complex networks of interacting species. When we investigate nutrients at the level of ecological networks, the patterns become more complicated. The structure of ecological networks may influence or be influenced by nutrition. By integrating nutritional information into networks, it is possible to assess system-level fluxes of nutrients between many organisms simultaneously. This may elucidate the importance of nutrients as drivers of trophic links (Figure S1).

By assessing the primary sources of different nutrients to a consumer, it is possible to evaluate the risk of extinction posed to that consumer by assessing the nutritional redundancy of its available resources (i.e., the alternative resources that might otherwise provide those nutrients). This is valuable for a broad range of ecological contexts; for example, assessing resource availability for species of conservation concern or nutritional complementarity of resources available to biocontrol agents as a means to encourage antagonistic interactions with pests. As discussed in greater depth later, this is also a viable method for predicting and assessing network rewiring since the consumer might select an alternative resource with a similar nutritional profile in the event of resource loss.

Spatial variation in nutrients affect ecological networks

The nutrients most important in a given network (e.g., those with the largest overall variation or those limited locally) will depend to some degree on the resources available and accessible in the environment. For example, a lipid limitation in higher trophic levels forces predators to disproportionately seek lipid-rich resources, more so than herbivores and omnivores which tend toward protein-rich resources instead (Al Shareefi & Cotter, 2019; Margalida, 2008; Raubenheimer et al., 2009; Wilder et al., 2013, 2016). Animal bodies typically contain a greater proportion of protein than lipid or carbohydrate, the latter exhibiting markedly less variation within invertebrate bodies (Cuff *et al.* 2021). High concentrations of non-structural carbohydrates can be detrimental and toxic to both the accumulating forager and any predator that feeds upon it (Schlotterer *et al.* 2009; Alcántar-Fernández *et al.* 2019), suggesting that surplus, not just limitation, could restructure networks. This is true of even protein, which can negatively affect fitness at higher concentrations (Anderson *et al.* 2020), and Bertrand's rule would suggest it is upheld for most chemicals (Raubenheimer, Lee, & Simpson, 2005). A greater degree of carbohydrate-focused foraging (i.e., disproportionately selecting high carbohydrate resources) has been suggested of omnivores and herbivores (Al Shareefi & Cotter 2019; Christensen *et al.* 2020), possibly a result of greater carbohydrate variation in plants. This pattern will, however, almost certainly vary between study systems.

An added complication to understanding how diet requirements affects networks, particularly in areas of nutritional deficit, is that some consumers regulate their nutritional requirements through selective consumption of particular nutrients from individual resources (Mayntz *et al.* 2005; Pekár *et al.* 2010). Hence, if a consumer is in need of a particular nutrient that is deficient in its resources, then predators, for example, could exhibit superfluous killing whereby they kill prey and only consume part of the prey body, which can have consequences for predator functional responses (Samu & Biro 1993; Maupin & Riechert 2001). These adaptive behaviours will, however, be mediated by nutrient availability at the ecosystem scale since some study systems are nutrient poor (e.g., deserts, caves and other systems with scarce photosynthetic flora are carbohydrate-poor; Peterson et al., 2016). Although the fauna of such systems may be physiologically adapted to rely less on those nutrients or efficiently extract them from suboptimal resources, nutrient limitation would be more likely to inflate the above-mentioned behaviours (Table 1). If, for example, a predator is foraging in a carbohydrate-limited system (i.e., one lacking basal carbohydrate or lacking prey that assimilate it from basal resources), we predict that it will likely disproportionately exploit those taxa which contain the highest proportion of carbohydrates should they be equally accessible to the other prey (Figure S2). In a nutritionally balanced system, however, the same predator might exhibit a far more balanced exploitation of prey taxa (i.e., evenness of interactions). Carbohydrate could also influence the structure of trophic networks containing many carbohydrate-rich taxa, such as sap- or nectar-feeding insects which interact regularly with carbohydrate-rich resources, due to an avoidance of large quantities of carbohydrate-rich prey (Schlotterer *et al.* 2009; Alcántar-Fernández *et al.* 2019). Importantly though, nutritional quality can vary at an intraspecific level with ontogeny (particularly so for holometabolous insects which often have higher lipid content), seasonality (e.g., in relation to reproduction or diapause; Raubenheimer, Mayntz, Simpson, & Toft, 2007) or imbalanced nutrient intake, leading to individual-level responses. Thus, individual-level networks may offer a more appropriate resolution for many nutritional studies.

Whilst nutrient-imbalanced environments (i.e., those containing resources suboptimal for a given consumer's nutrient requirements) may disadvantage foragers and generate distinct and predictable network structures,

an unfamiliar nutritional landscape will be evolutionarily mismatched to a forager’s innate nutrient-seeking behaviours (Al Shareefi & Cotter, 2019; Simpson & Raubenheimer, 2005). Animals in novel habitats may inefficiently forage for nutrients, at least initially, and their proliferation in that environment is likely pre-dicated by their nutritional or behavioural plasticity (Shik & Dussutour 2020). The evolutionary mismatch between introduced species and their novel environment would theoretically impose fitness consequences on that species (Al Shareefi & Cotter, 2019; Simpson & Raubenheimer, 2005). The incoming species’ lack of experience with the native resources and their provision, alongside potential phenological or ecological mismatches affecting the accessibility of these resources, would require a great degree of adaptability to optimally forage, or at least a flexible physiology. This principle may therefore explain the prevalence of dietary and nutritional generalism observed in many highly invasive species (Saveanu *et al.* 2017; Coogan *et al.* 2018; Krabbe *et al.* 2019; Shik & Dussutour 2020), possibly acting as a prerequisite for invasion success in certain contexts (Table 1). This nutritional niche hypothesis could theoretically be assessed in the same manner that other niches (e.g., climatic) have been assessed in an invasion context (Broennimann *et al.* 2007). Moreover, the impacts of invasive species may increase with the nutritional complementarity of the system they are invading, acting as a positive feedback loop that ultimately leads to more severe effects on local communities (Kaplan & Eubanks 2005; Zhang *et al.* 2012). Invasive species can also alter the nutritional environment by providing food resources, that can then affect nutrient availability for native or other invasive species (e.g., food for protection mutualisms between honeydew-producing hemipterans and red imported fire ants; Helms & Vinson, 2002; S.M. Wilder, Holway, Suarez, LeBrun, & Eubanks, 2011)

Nutrients can additionally explain long distance foraging, and migration choices and behaviours (Shaw 2016), and thus how regional species pools are translated into local ecological networks. For example, variation in the nutritional content of bamboo can drive seasonal migration of pandas (Nie *et al.* 2014). The extension of this nutritional naivety concept to the migration of taxa such as birds, butterflies, whales and other migrants widens its relevance to many additional ecological areas. These populations can show high fidelity toward migration sites despite passing unfamiliar but suitable sites *en route*, thought to confer the advantage of consistent foraging (Greenberg 1984; Shimada *et al.* 2020). This aversion to sites where the forager is naïve aligns with the notion that foragers, unless extreme generalists, or physiologically or behaviourally plastic, benefit from prior experience of resources in order to optimise nutrient acquisition. When considering species migrations for which the migrant lacks any familiarity with their destination, such species will likely need to be highly adaptive or generalist to optimally forage in that novel nutritional landscape, or sufficiently abundant that an adequate proportion of the population forage optimally by chance. Ballooning spiders offer one such example since they can travel hundreds of kilometres to stochastically arrive at nutritionally novel environments (Bell, Bohan, Shaw, & Weyman, 2005; Greenstone, 1990; Weyman, 1993). The nutritional consequence of species migration and introduction is also relevant to species that may consume newly arrived migrants at the destination site. Migrants can act as nutritional stores and flows between spatially distinct, local networks (Gresh *et al.* 2000; Schmitz *et al.* 2010; Bauer & Hoyer 2014). The import of locally scarce nutrients by migrants could have profound effects on the foraging decisions of local species resulting in potentially rapid rewiring of network structures. Moreover, introduced species may provide consistent or seasonal nutritional subsidies to native consumers post-colonisation (Ando *et al.* 2013; Tercelet *et al.* 2022), altering the nutritional landscape and, ultimately, the nutritional network.

The influence of nutrient availability on temporal dynamics of ecological networks

Dynamic effects of nutrients on network structure would perhaps be best exemplified in the study of network rewiring and robustness, in which primary extinctions drive the formation of new interactions or a series of cascading secondary extinctions (Kaiser-Bunbury *et al.* 2010). From a nutritional perspective, it is the balanced intake of, for example, lipids, proteins and carbohydrates that influences the persistence of individuals and populations (Toft & Wise 1999; Wilder 2011; Moatt *et al.* 2018), but also regulates their ability to respond to dynamic processes (Ponton *et al.* 2020). As such, we perceive the influence of nutrients on network dynamics as: (i) regulating the assembly and structure of the network, and thus the inherent sensitivity or susceptibility of the system to disturbances; and (ii) determining the responses of individuals, populations, communities, and thus networks to changes or dynamic processes.

As eluded to above in the context of nutrient availability and demand, taxa enriched with nutrients otherwise scarce in a network may have higher centrality, possibly explaining observations of preferential attachment models of network assembly (i.e., new vertices preferentially connecting to nodes with higher degrees may be a result of their nutritional novelty or importance; Barabasi, Albert, & Jeong, 1999; Olesen et al., 2008). The removal of such nodes, or central nutrient sources, from the network will thus impact a larger number of consumers than, for example, the removal of a node with either low quantities of nutrients or a low number of interactions. Network robustness is therefore likely to depend on the nutritional diversity and the evenness of resource taxon nutrient contents. Higher nutritional redundancy (i.e., resources having similar nutrient contents) will likely result in consumers relying on a greater number of resources for each nutrient, increasing network connectance. If alternative resources rich in a particular nutrient are not available when one such resource is removed, its consumers may be unable to meet their nutritional requirements and may become extinct. Current analyses neglect this nuance, instead redistributing interactions either randomly or based on node centrality and retaining consumers in the network so long as they are still connected to at least one extant resource.

Secondary extinctions are not the only response to node removal in networks, and it is possible for processes such as rewiring (i.e., changes to network topology such as interaction switching) to facilitate dynamic responses to either primary extinctions or temporal changes in species interactions (driven by, e.g., phenology, availability, resource quality). The nutritional complementarity of different resources is likely to be an important driver of rewiring since consumers require a balance of nutritional resources and will thus likely interact within a defined nutritional range. Such mechanistic rewiring rules could guide predictions, explain or contextualise predictions made without nutritional context or provide testable hypotheses for adaptive network analyses. This is particularly valuable in contexts such as conservation, restoration, invasions and perturbations (Kaiser-Bunbury *et al.* 2010; Raimundo *et al.* 2018; Maia *et al.* 2021), but the concept of rewiring is at the cutting edge of network science. By incorporating rewiring into adaptive network models, it is possible to generate testable predictions of adaptive responses to perturbations as is observed in natural systems (Raimundo *et al.* 2018; Maia *et al.* 2021).

Nutrient networks in practice: an inter-specific ecological network

Nutritional data are underrepresented in ecological networks, but one example is provided by Cuff, Tercel, Vaughan, et al., (2022). This study aimed to investigate nutrient-specific foraging in field-collected spiders using molecular dietary analysis, micro-scale macronutrient analysis and network-based null models. Nutritional data were determined via the MEDI protocol (Cuff 2021; Cuff *et al.* 2021). These data were integrated into a bipartite network of predator-prey interactions between spiders and their prey. Prey preferences were determined by comparison of null models based on prey density data against observed interactions (Vaughan *et al.* 2018). By bringing these data together, it was possible to investigate how nutrients affected interactions between spiders and their prey (additional methodological detail given in Supplementary Information 1). The nutritional data were integrated into the network by clustering taxa based on their mean macronutrient contents into 20 ‘tropho-species’ (i.e., taxonomy-independent clusters based on macronutrient contents). Through the integration of predator traits and prey density and, subsequently, nutrient data into this network, we can see how nutrients might affect network structure and complexity, but also how we can highlight the key motifs and structures of complex networks through the lens of nutrition (Figure 3).

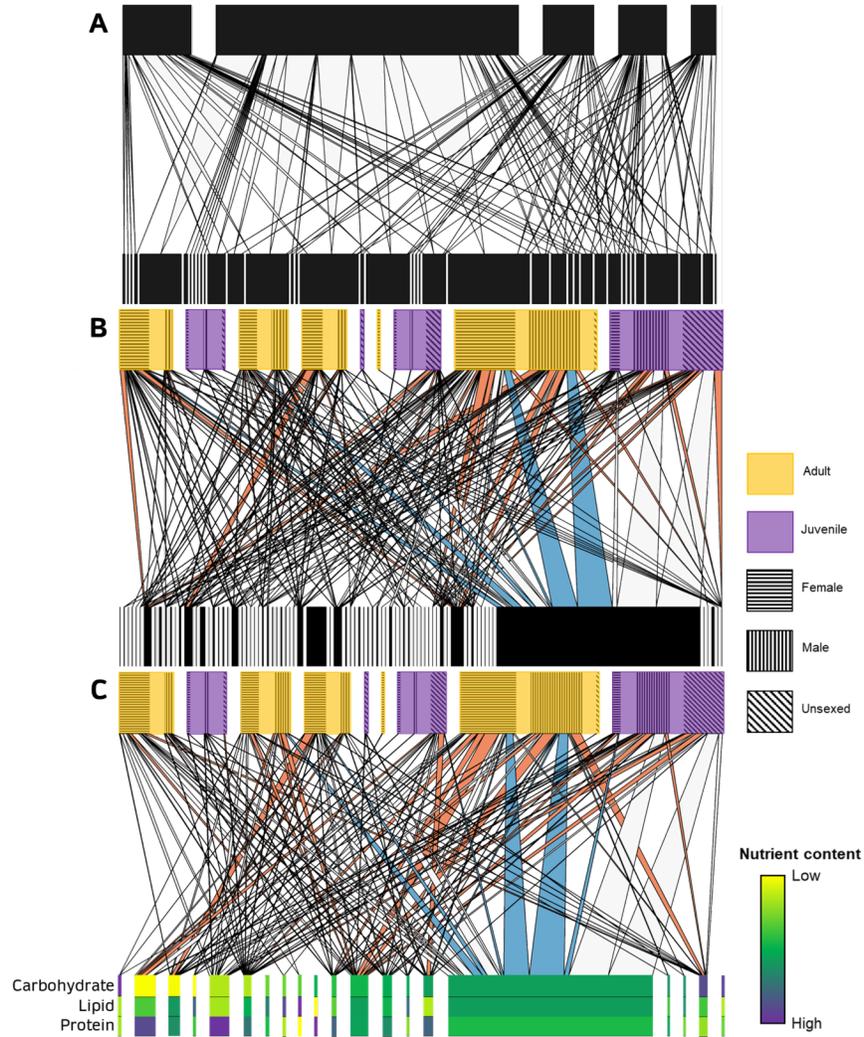


Figure 2: By integrating nutritional information into networks, it is possible to see which nutrients are disproportionately exploited by the consumers in that network. All three networks show spiders (top level) predating invertebrates (bottom level). A: Classic bipartite network; B: Detailed bipartite network with consumer traits incorporated; C: Nutritional bipartite network with consumer traits and resource nutrient contents incorporated. In this bipartite network, five spider genera are consuming invertebrate prey in cereal crops. The spider genera (upper level) are separated by life stage (red = adult, blue = juvenile) and sex (horizontal lines = female, vertical lines = male, diagonal lines = unsexed). Spider prey (lower level) are represented by tropho-species (i.e., prey taxa hierarchically clustered based on macronutrient content) to facilitate taxonomy-independent. Prey tropho-species are given in tritone blocks, each colour denoting the relative content of carbohydrate, lipid and protein from top to bottom, respectively, and yellow through green to purple representing increasing content in each nutrient. The width of links between the two trophic levels at the top denotes the relative the relative exploitation of the lower resource, and at the bottom denotes the relative abundance of that resource in the local community. Red and blue links denote preference and avoidance of that resource by the linked consumer group, respectively, based on comparison of observed predation frequency with that expected by null models based on the relative abundance of the prey. By presenting the bipartite network as such, it is possible to investigate differences in nutrient exploitation by spider genera, sexes and life stages. Networks generated using bipartite (Dormann *et al.* 2008) and

econullnetr (Vaughan *et al.* 2018) in R (R Core Team 2021). The methods used to generate the data are presented by Cuff, Tercel, Drake, et al., (2022) and Cuff, Tercel, Vaughan, et al., (2022) and summarised in Supplementary Information 1.

Here we show that by simplifying representation of network nodes as ‘tropho-species’ based on nutritional similarity, we can disentangle complex ecological networks and illuminate potential nutrient-mediated effects that drive their contemporary dynamics. In this example we see reduced partner diversity and link density, at least compared to the complex network without nutrient data (Figure S3). While this could reflect the reduced resource diversity (i.e., there are fewer tropho-species than Linnean taxa), it demonstrates that some of the prey consumed are nutritionally similar, or nutritionally redundant. The reduced vulnerability and increased generality in the nutritional network also reflect the nutritional redundancy of the prey therein, indicative of a network that appears, at least in terms of macronutrients, robust to extinctions. The integration of trait data into analyses of trophic interactions has gained increasing traction over the last decade given its power in predicting and rationalising interactions (Green & Côté 2014; Spitz *et al.* 2014; Brose *et al.* 2019). The above approach, treating nutrients as traits, shows that this is a viable strategy for the integration of nutritional data into networks. The ecological relevance of the nutritional redundancy of different taxa is, of course, dependent on the plausibility of interactions between the predator and the nutritionally similar prey which can be ecologically distinct despite nutritional similarity (e.g., ichneumonid wasps and linyphiid spiders are in the same nutritional cluster despite being behaviourally and ecologically distinct). Regardless, the integration of nutrients by means of the tropho-species concept increases the information present in the network, at least from a nutritional perspective, whilst simultaneously reducing the complexity, facilitating the streamlined assessment of nutritional dynamics in this system. Whilst this simplified data-rich approach neglects taxonomy, it facilitates a functional analysis of the impact of nutrients on network structure.

Such networks can, however, be represented in many different ways. As discussed, and hypothetically presented above (also see Figure S1), the flow of nutrients between resources and consumers could be presented by representing the proportional transfer of nutrients as interaction weights (Figure 3, S4 & S5). In this way it is possible to visually compare the overall transfer of each nutrient (i.e., protein is transferred in greater quantities than carbohydrate in Figure 3, but this may differ in, for example, plant-herbivore networks), but also how the degree of each node may be linked to its nutrient weighting in one or more of the networks. This representation of nutrients could be streamlined by integrating all three networks into a multilayer structure, but this requires careful consideration or simplification to avoid visual overcrowding and obfuscation of the overall patterns. An alternative simplification can be achieved by aggregating resources together and instead representing interaction between consumers and individual macronutrients (Figure S6). Whilst this neglects the ecological context of interactions with specific taxa, it is a valuable means for assessing the relative importance of each macronutrient in the foraging of individual consumers.

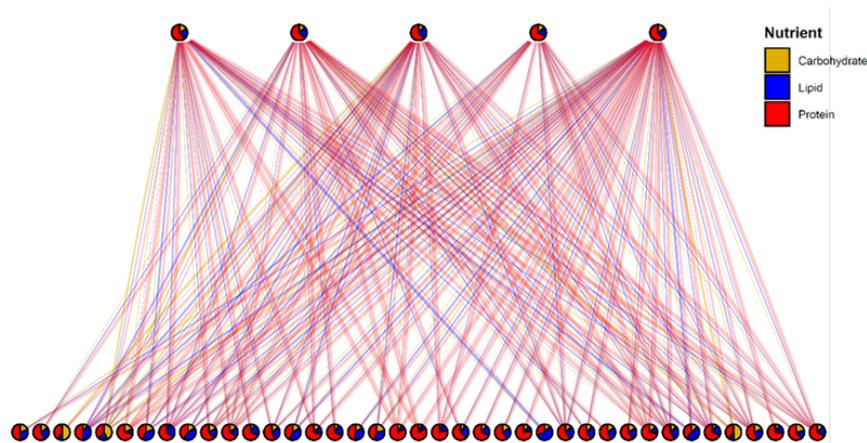


Figure 3: By assessing network structure with interactions weighted based on the transfer of each individual nutrient, it is possible to visualise how nutrients transfer through ecological networks, the importance of each nutrient for different consumers and how rich the resources exploited by each consumer are in each nutrient. This network represents the exchange of all three nutrients (yellow, blue and red representing carbohydrate, lipid and protein, respectively) between the spiders represented in Figure 2 (top level; each a different spider genus, their mean macronutrient intakes represented by the pie chart proportions of each colour) and their prey (bottom level; their mean macronutrient content represented by the pie chart proportions of each colour). Network generated using igraph (Csardi & Nepusz 2006), ggplot2 (Wickham 2016), ggnetwork (Briatte 2021) and scatterpie (Yu 2021) in R (R Core Team 2021). The same network is presented with links denoting just carbohydrate enrichment in Figure S4.

Limitations of nutritional networks

Whilst nutrients may be an important driver of interactions, they are not an outright determinant of them. Unless alternative resources with similar nutritional profiles are available, the nutrient-dependence of interactions may be overridden (Rendon *et al.* 2019) and more concertedly led by factors such as predator hunger state (Lang & Gsodl 2001), prey abundance, or prey traits including dispersal (Pastorok 1981), camouflage (Endler 1978), defences (Provost *et al.* 2006), escape capability (Lang & Gsodl 2001; Provost *et al.* 2006) or size (Bence & Murdoch 1986; Downes 2002; Turesson *et al.* 2002). Nutrients can factor into foraging choices at different stages of the foraging process too, from the selection of specific prey, to the consumption of different quantities of different prey or the extraction of specific nutrients (Pekár *et al.* 2010; Kohl *et al.* 2015), which might be difficult to reliably integrate into network datasets. A further complexity is that nutrient preferences may also change based on sex, life stage (Al Shareefi & Cotter 2019; Cuff *et al.* 2022c), phenology (Raubenheimer *et al.*, 2007) and any other factor affecting nutritional requirements or foraging ability. Networks must thus integrate context-specific nutritional data and relevant forager meta-data wherever possible to account for this otherwise unchecked variation.

The methods with which networks are constructed and trait data included are also important to consider. There are streamlined and cost-effective protocols for nutrient quantification (Cuff *et al.* 2021), but many alternative methods exist, each with different advantages, and have been recently reviewed (Zaguri *et al.* 2021a, b). Newer techniques for network construction such as DNA metabarcoding present several novel challenges already (Cuff *et al.* 2022d), but in a nutritional context some of these issues can be compounded. There is currently a lack of appropriate protocols for parallel macronutrient and nucleic acid extraction from the same individual, meaning these networks neglect individual-level interaction data. Metabarcoding-based networks can also neglect the life stage and sex of their nodes (Nestel *et al.* 2016) and fail to distinguish nutritionally significant interaction types such as scavenging, secondary predation, accidental consumption, parasitism and symbiosis (Greenstone, Rowley, Weber, Payton, & Hawthorne, 2007; Paula *et al.*, 2015; Tercel, Symondson, & Cuff, 2021; von Berg, Traugott, & Scheu, 2012). Many traditional network construction methods, such as transect observations, may also neglect some of this information despite its importance for ecological interactions.

Conclusions

We have highlighted the importance of nutrients in ecological interactions and how we expect them to affect the structure and function of ecological networks. With increased integration of nutritional data into such networks, whilst heeding the auxiliary hypotheses underlying their inclusion, the complexity and explanatory power of those networks could advance considerably, including predictions of rewiring in adaptive networks. This synthesis is focused primarily on trophic interactions, but nutrients may carry profound implications for most other interaction types. Mutualisms such as pollination and seed dispersal ultimately rely on nutritional rewards which may differ in their attractiveness not only based on quantity, but complementarity and quality. Equally, the viability and success of host-parasitoid interactions are constrained by the adequacy of nutritional supplementation of developing parasitoids by their hosts' body. Even social and sexual interactions

may be heavily impacted by nutrients (Lihoreau *et al.* 2014, 2017); for example, trophallaxis in ants (i.e., the provision of regurgitated gut contents and chemical cues inter-orally between ant individuals) may confer nutritional benefit, or the nutritional content of nuptial gifts presented by, for example, nurseryweb spiders (*Pisaura mirabilis*), may be an important determinant of the success of courtship. Whilst it is intuitive to speculate on the importance of nutrients in these interactions, many such phenomena are entirely uncharacterised from a nutritional perspective.

To elucidate the nutritional dynamics of these networks, novel approaches must be integrated into network ecology for increasingly complex and powerful network construction. Network ecology, if used objectively, can overcome the dogma of presumed interactions by assessing and comparing interactions with unbiased and broad network construction methods (e.g., the assessment of seed dispersal by Evans *et al.*, 2011). When applying these principles in system-wide interaction networks alongside nutrient data, this will provide nutritional context and rationale to interactions, but may also advance our understanding of nutritional ecology by objectively and holistically characterising how nutrients dynamically move through ecological networks.

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